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**MONOPHYLY VERSUS THE CEPHALASPIDEA
(GASTROPODA, OPISTHOBRANCHIA)
WITH AN ANALYSIS OF TRADITIONAL CEPHALASPID CHARACTERS
(**)**

KEY WORDS: Cephalaspidea, Opisthobranchia, systematics, cladistics, phylogeny, homoplasy, parallelism, characters.

Abstract

The opisthobranch order Cephalaspidea is well-recognized as an unnatural, paraphyletic group characterized by «evolutionary trends» toward reduction and loss of many features. A survey of 35 key classifications and published phylogenograms involving cephalaspids revealed a general lack of morphological definition for the order and the tenacious use of traditional characters. Of 49 frequently-used characters, 44 (90%) are problematic for use in modern phylogenetic (cladistic) analyses due to reductive nature, non-homology, incompleteness, or other grounds. Claims of «rampant parallelism» involving a majority of these characters are based on *a priori* decisions and are therefore presently unjustified. The few consistent family groups in published phylogenograms are most strongly supported by characters correlated with diet, and may therefore also be open to question. Successful resolution of the phylogeny of these and other «lower heterobranchs» will require critical reevaluation of cephalaspid morphology to determine an improved set of taxonomically informative, homologous characters. New areas of investigation are proposed.

Riassunto

L'ordine dei Cephalaspidea è generalmente considerato un raggruppamento innaturale, parafiletico, caratterizzato da «indirizzi evolutivi» che tendono ad una riduzione e perdita di molti caratteri. L'analisi di 35 chiavi di classificazione e degli alberi filogenetici recentemente pubblicati che coinvolgono i cefalaspidei indica una carenza nella definizione morfologica dell'ordine ed il costante uso di caratteri tradizionali.

Dei 49 caratteri più frequentemente usati, 44 (il 90%) sono difficili da utilizzare nella moderna analisi cladistica a causa della loro natura riduttiva, non omogeneità, incompletezza o altro.

Le ipotesi di un «parallelismo ascendente» fatte per la maggior parte sulla base di questi caratteri appaiono sostenute da decisioni aprioristiche e sono dunque, al momento, ingiustificate. Inoltre i pochi raggruppamenti tassonomici di un certo valore sono per la maggior parte sostenuti da caratteri collegati con la dieta e dunque discutibili.

Un'analisi corretta della filogenesi di questo, come di altri gruppi, appartenenti ai «bassi eterobranchi» richiederà una critica rivalutazione della loro morfologia, per definire insiemi di caratteri omologhi d'interesse tassonomico.

A tal proposito, vengono qui presentate nuove aree d'indagine.

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Introduction

Within the opisthobranchs, the Order Cephalaspidea [=Bullomorpha, Tectibranchiata (in part), «bubble-shells»] is morphologically mosaic as a group, and is traditionally considered «basal», or «transitional» between typical prosobranchs and «higher» opisthobranchs (e.g., BOETTGER, 1955; SCHMEKEL, 1985). Systematics within the order (as well as for the order itself) is currently based upon anagenetic organizational grades, phenetic similarities and «evolutionary trends» rather than upon distinct synapomorphies. Any such assemblage does not meet modern phylogenetic standards and may not be monophyletic. Several authors (e.g., RUDMAN, 1972; GOSLINER, 1992) have already suggested that this is true of Cephalaspidea.

Cephalaspidea was originally introduced by P. FISCHER (1883b: 550) as a subdivision (with Anaspidea and Notaspidea) of Tectibranchiata CUVIER, 1812. The new group of nine families (Fig. 1) was distinguished by the presence of «un large disque céphalique». It is now generally agreed (e.g., BRACE, 1977a,b) that this and other features of «typical» cephalaspid anatomy are the products of extensive ecophenotypic modification related to burrowing through soft sediment, a habit successfully exploited by most extant members of the present order. These kinds of features could conceivably have evolved in parallel in unrelated taxa under similar circumstances, and as such, may not reflect phylogenetic relationships. Similar statements have also been made for characters associated with diet (MIKKELSEN, 1989, 1990), reduction in body size (GHISELIN, 1963, 1966; HASZPRUNAR, 1985), and loss of the shell (GOSLINER & GHISELIN, 1984). The apparent high incidence of homoplasy in opisthobranchs led GOSLINER & GHISELIN (1984: 263-264; also GOSLINER, 1981, 1991) to contend that «rampant parallelism» made it «difficult, if not impossible» to resolve opisthobranch relationships using modern cladistic methods. Although terminology has occasionally implied the use of phylogenetic techniques (GOSLINER, 1978, 1991; HASZPRUNAR, 1988), few rigorous analyses of opisthobranchs by modern methods have appeared. WILLAN's (1987) treatment of Notospidea is a notable exception.

PATTERSON (1989: 484) contended that «success in systematics requires three things: good data (characters), sound methods of analysis, and criteria for evaluating the results». Phenetic analytical approaches have been unsuccessful in resolving the continual problems in cephalaspid systematics. Further review presented here implicates a second, more basic deficiency, i.e., the tenacious use of traditional characters, most of which are problematic in cephalaspids. This study suggests that successful resolution of this phylogeny may lie more in rigorous character selection than in the use of alternate methodologies.

Material and Methods

Thirty-five key works in cephalaspid systematics were selected and analyzed for agreement in classification or proposed phylogeny presented, the character used (if given), any consistent family groups, and any synap-

FISCHER (1883b)

Current placement

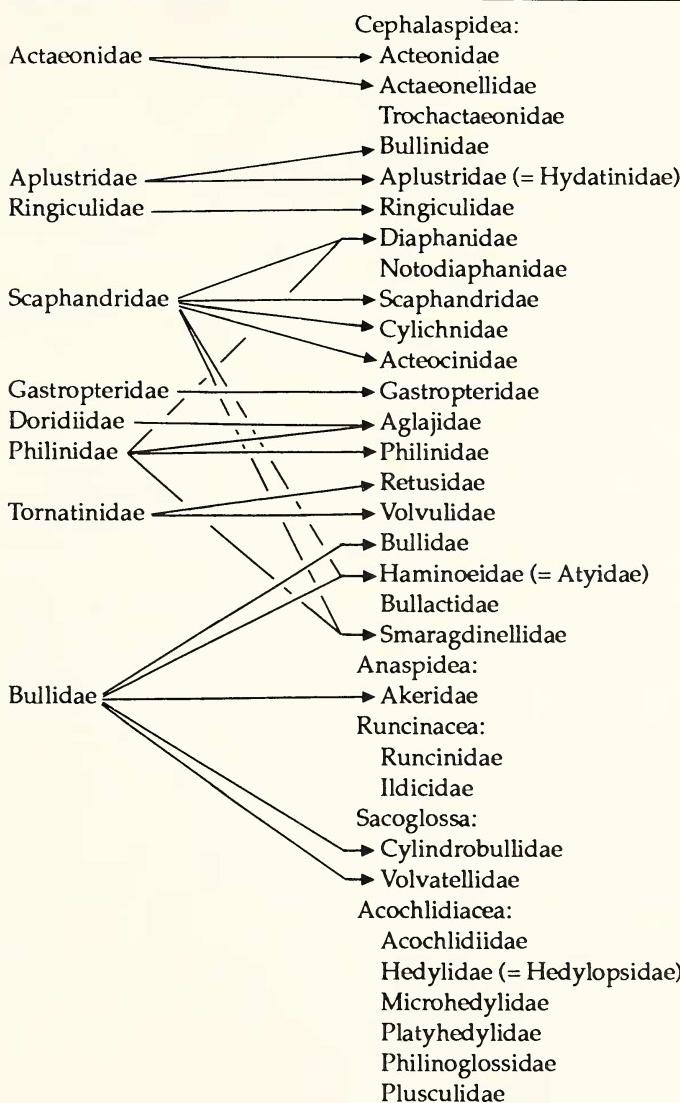


Figure 1. The 31 «traditional» cephalaspid families and their current taxonomic placement (based mainly on Boss, 1982), as derived from FISCHER's (1883b) original Cephalaspidida.

omorphies defining family groups. Among them were 17 comprehensive and/or well-recognized classifications [FISCHER, 1883b; PILSBRY, 1894-1896; THIELE, 1931; ODHNER, 1939; ZILCH, 1960; TAYLOR & SOHL, 1962; ODHNER in FRANC, 1968; NORDSIECK, 1972; ABBOTT, 1974; THOMPSON, 1976; MARCUS, 1977; BOSS, 1982; LONG, 1983; VAUGHT, 1989; SABELLI, *et al.*, 1990-1992; combined Austrian scheme (HASZPRUNAR, 1985; SALVINI-PLAWEN, 1988, 1991a,b); combined Russian scheme (MINICHEV & STAROBOGATOV, 1979a,b; GOLIKOV & STAROBOGATOV, 1989)], and all known proposed phylogenograms (18) indicating cephalaspid relationships [FISCHER, 1883b: 551; COSSMANN, 1895: table; PILSBRY, 1896: vii; GUIART, 1901: 201-202; BOETTGER, 1955: fig. 1; MORTON, 1963: fig. 2; GHISELIN, 1966: fig. 7; SALVINI-PLAWEN, 1970: fig. 1; BEEMAN, 1977: fig. 15; GOSLINER, 1978: pl. 22, fig. 36 (unpublished thesis); RUDMAN, 1978: figs. 2-6; KANDEL, 1979: fig. 2-3; EDLINGER, 1980: fig. 9; HASZPRUNAR, 1985: fig. 5; SCHMEKEL, 1985: fig. 17; POULICEK *et al.*, 1991: fig. 1; SALVINI-PLAWEN, 1991a: fig. 15; SALVINI-PLAWEN, 1991b: fig. 5].

The phylogenograms presented in Figs. 3-5 are redrawings of previously published trees, and do not represent original, cladistically-derived results.

Results and Discussion

Additions and subtractions - a history of Cephalaspidea

Cephalaspidean taxonomic history has been one of repeated inclusions and exclusions, expansions and restrictions. Within the genera and subgenera of FISCHER's (1883b) original taxon are found the bases of most (20) of the 31 families which have been assigned to Cephalaspidea since FISCHER's time (Fig. 1). Subsequent anatomical studies by GUIART (1901), BERGH (1900-1908) and others induced a proliferation of family-level groups, accompanied by a dizzying rate of taxonomic rearrangement [Fig. 2; PILSBRY, 1894-1896 (10 families); THIELE, 1931 (14); BOETTGER, 1955 (15, excluding Pyramidellidae and Euthecosomata); ZILCH, 1960 (15); TAYLOR & SOHL, 1962 (15); ODHNER in FRANC, 1968 (13); THOMPSON, 1976 (16); MARCUS, 1977 (18); BOSS, 1982 (13); LONG, 1983 (23); VAUGHT, 1989 (16); SABELLI *et al.*, 1990-1992 (13)]. Most of the activity has focussed on a limited number of families moving back and forth between Cephalaspidea and other opisthobranch groups: (1) Akeridae to Anaspidea (GUIART, 1901; THOMPSON & SEAWARD, 1989), (2) Volvatellidae/Cylindrobullidae to Sacoglossa (=Ascoglossa; EVANS, 1950; MARCUS, 1982), (3) 4-6 families of meiofaunal «sand-nudibranchs» to their own orders, Acochlidiae and Philinoglossacea, or (in part) to Sacoglossa (ODHNER, 1939; WAWRA, 1979; MARCUS, 1982; SALVINI-PLAWEN, 1973), and (4) Runcinidae/Ildicidae to their own order Runcinacea (ODHNER, 1939; BURN, 1963; ODHNER in FRANC, 1968; GHISELIN, 1963; THOMPSON & BRODIE, 1988).

This continual shifting is partially due to new analyses and new data, but it also stems from our lack of a solid morphology-based definition for the order. High variability is the rule: shell external, internal or absent; thick or thin, involute or with spire exposed; operculum present or absent; mantle cavity anterior or posterior, enclosed or open; parapodia present or absent; gizzard present or absent; jaws usually absent; radula usually pres-

ent; penis usually retractile; etc. The cephalic shield and Hancock's organ once regarded as synapomorphies for Cephalaspidea (e.g., SCHMEKEL, 1985) are no longer warranted in view of the above-mentioned removals of controversial taxa.

In perhaps the most dramatic rearrangement to date (Table 1), two Austrian workers (HASZPRUNAR, 1985; SALVINI-PLAWEN, 1988, 1991a,b) have suggested removing six families — Acteonidae, Bullinidae, Aplustridae, Ringiculidae, Diaphanidae, and Notodiaphanidae — from the Cephalaspidea mainly on the basis of shared symplesiomorphies (streptoneury, pallial gonduct, lack of gizzard). Two new groups have been proposed: (1) Architectibranchia, a «conservative» paraphyletic superorder (HASZPRUNAR, 1985; SALVINI-PLAWEN, 1991b), and (2) Dystectibranchia (including several «non-cephalaspid» groups), «an interrelated stock with mosaic evolution» (SALVINI-PLAWEN, 1991a: 24). The remaining cephalaspid families are treated as the order Bullomorpha, in the derived superorder Paratectibranchia (HASZPRUNAR, 1985; SALVINI-PLAWEN, 1991b). [SALVINI-PLAWEN (1991a) altered this, treating Paratectibranchia as another paraphyletic basal group.] Major divisions of Cephalaspidea reminiscent of this were earlier implied, although never formally proposed, by GUIART (1901; for Acteonidae), GHISELIN (1966; for Acteonidae, Aplustridae), BEEMAN (1978; for Acteonidae), GOSLINER (1978; for Acteonidae, Bulinidae, Aplustridae, Ringiculidae), EDLINGER (1980: fig. 9; for Acteonidae, Aplustridae, Diaphanidae), GOSLINER & GHISELIN (1984: fig. 1; for Acteonidae), and SCHMEKEL (1985: figs. 2,7,9,17; for Acteonidae, Ringiculidae).

HASZPRUNAR (1985) and SALVINI-PLAWEN (1988, 1991a,b) did not define the familial contents nor characteristics of their paratectibranch group Bullomorpha. By process of elimination, 8 families are inferred: Scaphandridae, Philinidae, Gastropteridae, Aglajidae, Retusidae, Bullidae, and Haminocidae/Smaragdinellidae. Runcinidae/Ildicidae and Philinoglossidae/Plusculidae were also included here (and Retusidae and Philinidae confirmed) by HUBER (1987). From discussion of the larger Paratectibranchia (HASZPRUNAR, 1985), it can be deduced that herbivory and an anterior armed gizzard are regarded as plesiomorphic for Bullomorpha. Beyond this, synapomorphies defining the group have not been recognized and therefore the question of monophyly, as implied by the trees presented by HASZPRUNAR (1985: fig. 5) and SALVINI-PLAWEN (1991a: fig. 15; 1991b: fig. 5), remains open.

Russian workers (MINICHEV & Starobogatov, 1979a,b; GOLIKOV & STAROBOGATOV, 1989) have independently taken steps similar to those of the Austrians, based almost entirely on reproductive morphology: (a) Ringiculidae in subclass Sinistrobranchia (=Allogastropoda), (b) Acteonidae and Aplustridae in subclass Opisthobranchia: Phyllidiiformii, and (c) the remaining cephalaspids (together with various traditional anaspids, sacoglossans, and notably Diaphanidae/Notodiaphanidae) in Opisthobranchia: Bulliformii. Since the groups proposed by the Russian school were largely undefined, it is impossible to discuss this radical classification further.

Eighteen phylogenograms defining relationships of and/or among cephalaspideans have appeared in the literature (see list under Materials & Methods). The three earliest versions (FISCHER, 1883b; COSSMAN, 1895;

PILSBRY, 1896) were based on shells, «hard parts» (radula, jaws, gizzard plates), and gross external anatomy, one accounted for stratigraphic appearance of fossil taxa (COSSMANN, 1895), one was restricted to a single superfamily (RUDMAN, 1978), three others were primarily single-organ-system analyses (BOETTGER, 1955; GHISELIN, 1966; EDLINGER, 1980), three were slight modifications of previous trees [SALVINI-PLAWEN, 1970 (of BOETTGER, 1955); BEEMAN, 1977 (of GHISELIN, 1966); POUICEK *et al.*, 1991 (of GHISELIN, 1966)], and one concerned only the relationship of Cephalaspidea to other opisthobranch orders (SCHMEKEL, 1985). None of the 18 trees was generated through cladistic methods.

The three most comprehensive treatments to date [GHISELIN, 1966; SALVINI-PLAWEN's 1970 modification of BOETTGER, 1955; GOSLINER, 1978; redrawn here in cladistic fashion for purposes of discussion and comparison (Figs. 3-5)], are unsatisfactory for a number of reasons. BOETTGER's (1955) tree has been criticized (GOSLINER, 1978, 1991; GOSLINER & GHISELIN, 1984) for being based on the shell and nervous system, both believed to contain many characters showing parallel evolution (associated with loss of the shell or reduction in body size). SALVINI-PLAWEN's (1970 updated version of BOETTGER (notably also removing modern families from nodal ancestral positions) still left six major clades (grades) radiating from a single node (Fig. 3). GHISELIN's (1966) originally confusing tree was based largely on a single system (reproductive anatomy), distinguished many opisthobranch groups by undefined «similarities», and united most of the cephalaspideans through traditional «hard-parts» (gizzard plates; Fig. 4). Finally, GOSLINER's (1978) interpretation, although based on a more complete dataset and employing qualitative weighting of characters, left an unresolved octochotomy (in figure; pentachotomy according to text) adding little new information on cephalaspid interrelationships (Fig. 5). Most importantly in modern phylogenetic terms, the Cephalaspidea itself is not monophyletic in any of these three phylogenograms.

Paraphyly of the Cephalaspidea is not a new discovery. Relative to other opisthobranchs, PILSBRY (1985: 134) early recognized the Tectibranchiata (= Cephalaspidea + Anaspidea + Notaspidea) as «a synthetic type, from which in the remote past, the Nudibranchiata and Pulmonata have no doubt been derived». With the breakup of Tectibranchiata by the 1960's [or the reduced but similar Pleurocoela of THIELE, 1931; not Tectibranchia *sensu* HASZPRUNAR (1935: 33) nor SALVINI-PLAWEN (1991a: 23)], the Cephalaspidea assumed the role of the «ancestral stock» of the opisthobranchs (GOSLINER, 1978; GOSLINER & GHISELIN, 1984). The phylogenograms of BOETTGER (1955: fig. 1) and SCHMEKEL (1985: fig. 17) are prime examples of this view, with the clearly-paraphyletic Cephalaspidea defined mainly by sympleiomorphies. Although the Austrian-advocated division considers most of the cephalaspids as members of the presumably-monophyletic Bullomorpha, their Architectibranchia and Dystectibranchia still occupy the paraphyletic position once held by the entire Tectibranchiata.

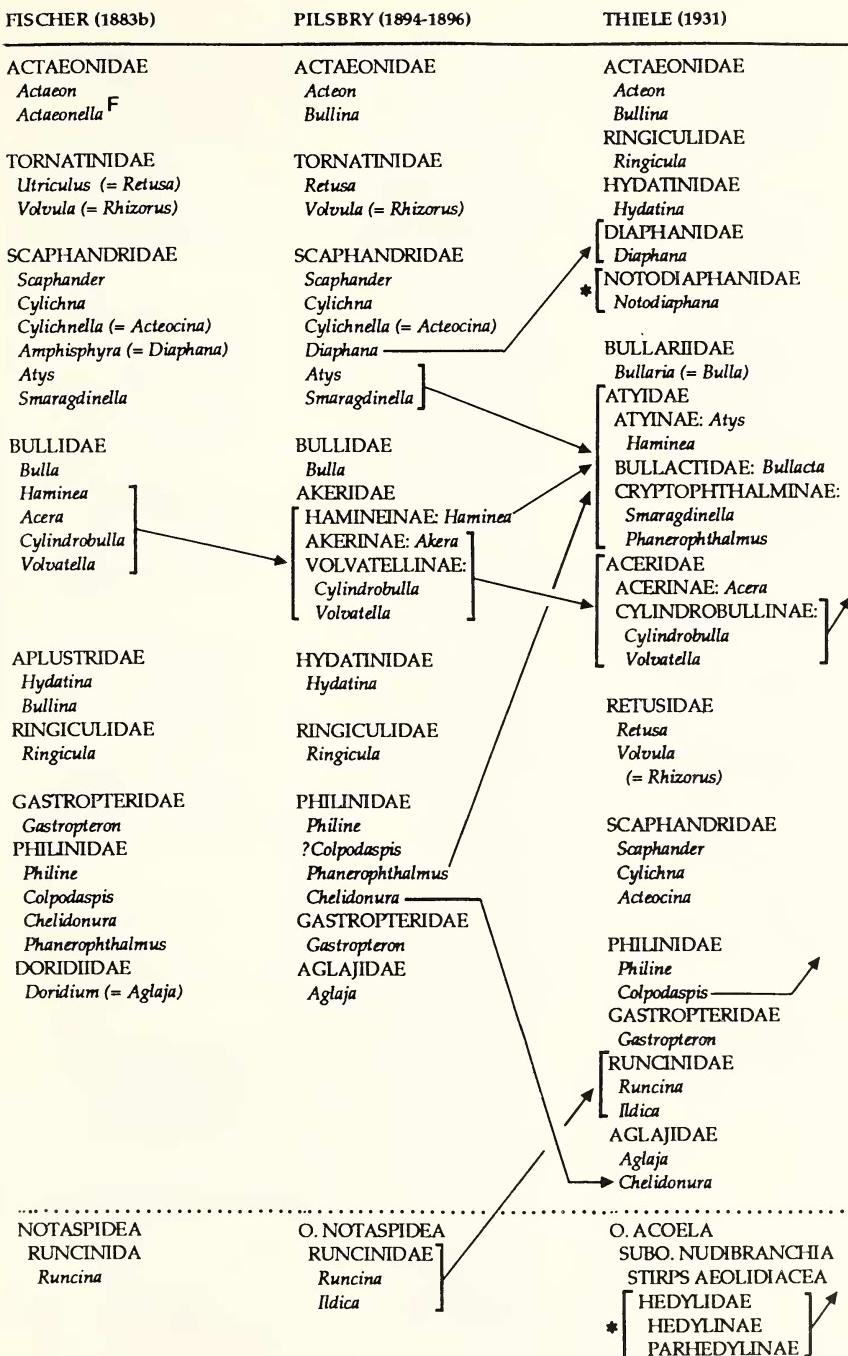
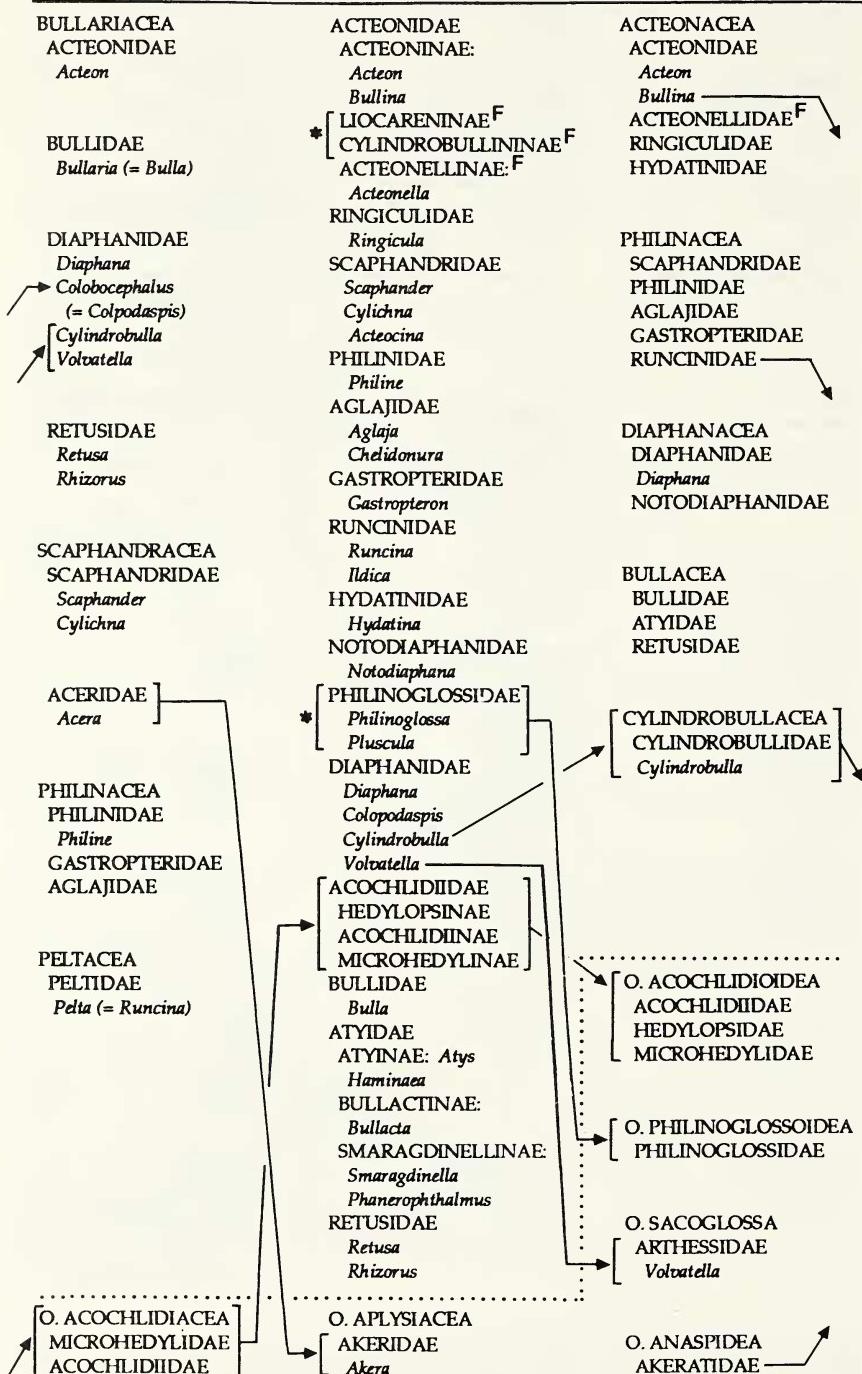


Figure 2. Cephalaspid classification by key authors, with superfamilies (if any), families, and representative genus-level taxa. Arrows indicate movement of genera, creation of new families, and movement of taxa in and out of Cephalasidea. Non-cephalaspid groups below dotted line. F = exclusively-fossil taxa. * = first appearance of new additions.

ODHNER (1939)

ZILCH (1960)

TAYLOR & SOHL (1962)



ODHNER in FRANC (1968)

NORDSIECK (1972)

ABBOTT (1974)

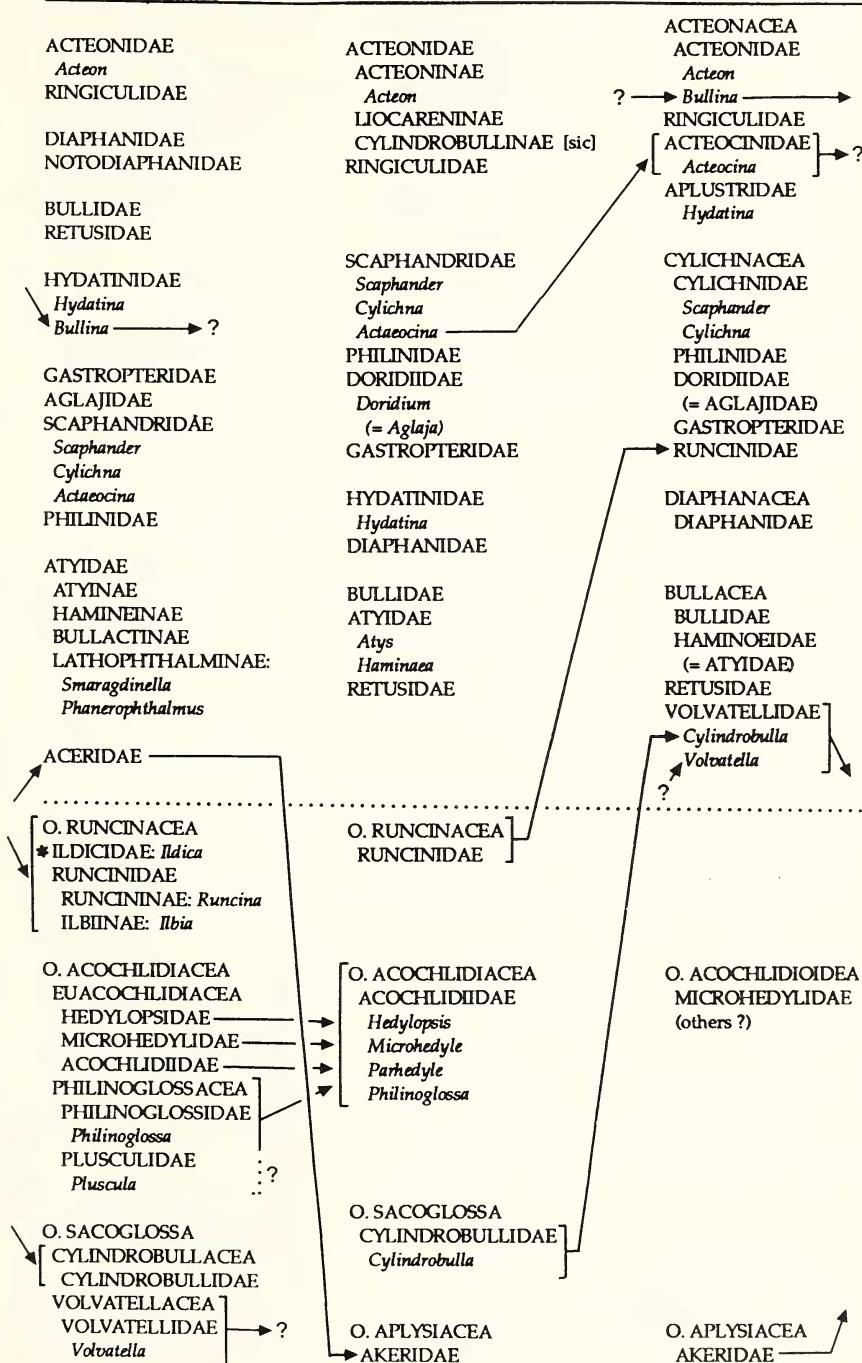


Figure 2 (continued)



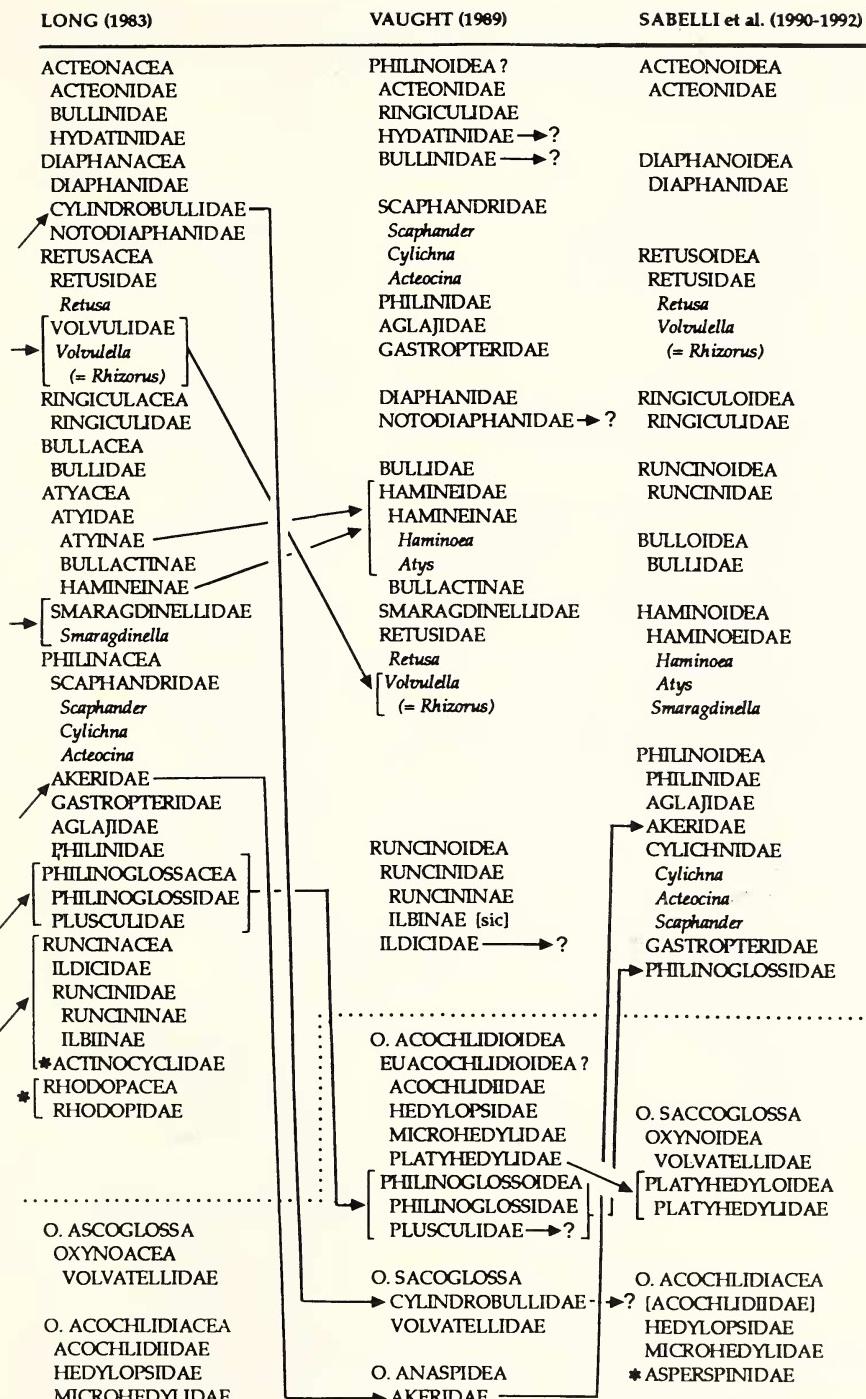


Figure 2 (continued)

Table 1. New classifications of «cephalaspid» by the Austrian school (HASZPRUNAR, 1985; SALVINI-PLAWEN, 1988, 1991a,b) and the Russian school (MINICHEV & STAROBOGATOV, 1979a,b; GOLIKOV & STAROBOGATOV, 1988). Included families inferred (where indicated) through name of superfamilial taxon and currently-accepted groups. * = «non-cephalaspid», included families not listed here.

AUSTRIAN SCHOOL	RUSSIAN SCHOOL (families inferred)
SCL. HETEROBRANCHIA	SCL. SINISTROBRANCHIA
COHORS TRIGANGLIONATA	SUPERO. ARCHITECTONICIFORMII*
SUPERO. ALLOGASTROPODA*	SUPERO. MELANELLIIFORMII*
COHORS PENTAGANGLIONATA	SUPERO. PYRAMIDELLIFORMII
SUPERO. ARCHITECTBRANCHIA	O. RINGICULIFORMES
O. ACTEONOIDEA	SUBO. RINGICULOIDEI
ACTEONIDAE	RINGICULIDAE
BULLINIDAE	O. PYRAMIDELLIFORMES*
HYDATINIDAE	SCL. OPISTHOBRANCHIA
O. RINGICULOIDEA	SUPERO. PHYLDIIFORMII
RINGICULIDAE	O. ACTEONIFORMES
SUPERO. DYTECTIBRANCHIA	ACTEONIDAE
O. DIAPHANOIDEA	HYDATINIDAE
DIAPHANIDAE	O. PLEUROBRANCHIFORMES*
NOTODIAPHANIDAE	O. PHYLLIDIIFORMES*
O. SACOGLOSSA	O. TRITONIFORMES*
CYLINDROBULLIDAE	SUPERO. POLYBRANCHIFORMII*
VOLVATELLIDAE	SUPERO. BULLIFORMII
(others)	O. BULLIFORMES
O. ACOCHLIDIOMORPHA	SUBO. DIAPHANOIDEI
ACOCHLIDIIDAE	DIAPHANIDAE
HEDYLIDAE	NOTODIAPHANIDAE
MICROHEDYLIDAE	SUBO. BULLOIDEI
PLATHEDYLIDAE	BULLIDAE
O. RHODOPEMORPHA*	SUBO. SCAPHANDROIDEI
SUPERO. PARATECTIBRANCHIA	SCAPHANDRIDAE
O. THECOSOMATA*	PHILINIDAE
O. BULLOMORPHA (families inferred)	GASTROPTERIDAE
SCAPHANDRIDAE	AGLAJIDAE
PHILINIDAE	SUBO. PHILINOGLOSSOIDAE
GASTROPTERIDAE	SUBO. HAMINEOIDEI
AGLAJIDAE	HAMINEOIDAE
RETUSIDAE	O. RUNCINIFORMES
BULLIDAE	RUNCINIDAE
HAMINEOIDAE	ILDICIDAE
SMARAGDINELLIDAE	O. APLYSIIFORMES
RUNCINIDAE	AKERIDAE
ILDICIDAE	(others)
PHILINOGLOSSIDAE	O. PNEUMODERMATIFORMES*
PLUSCULIDAE	O. TAMANOVALVIFORMES
O. ANASPIDEA	SUBO. CYLINDROBULLOIDEI
AKERIDAE	CYLINDROBULLIDAE
(others)	SUBO. VOLVATELLOIDEI
O. GYMNOSOMATA*	VOLVATELLIDAE
COHORS ELEUTHEROBRANCHIA*	(others)
COHORS CYNMORPHA*	SCL. DEXTROBRANCHIA
COHORS PULMONATA*	SUPERO. UMBRACULIFORMII*
	SUPERO. ACOCHLIDIIFORMII
	O. ACOCHLIDIIFORMES
	SUBO. PLATHEDYLIDAE
	PLATHEDYLIDAE
	SUBO. HEDYLOPSOIDAE
	HEDYLOPSIDAE
	MICROHEDYLIDAE
	SUBO. ACOCHLIDIOIDEI
	ACOCHLIDIIDAE
	(others)
	SUPERO. PERACLIFORMII*
	SUPERO. ONCHIDIIFORMII*
	SCL. PULMONATA*

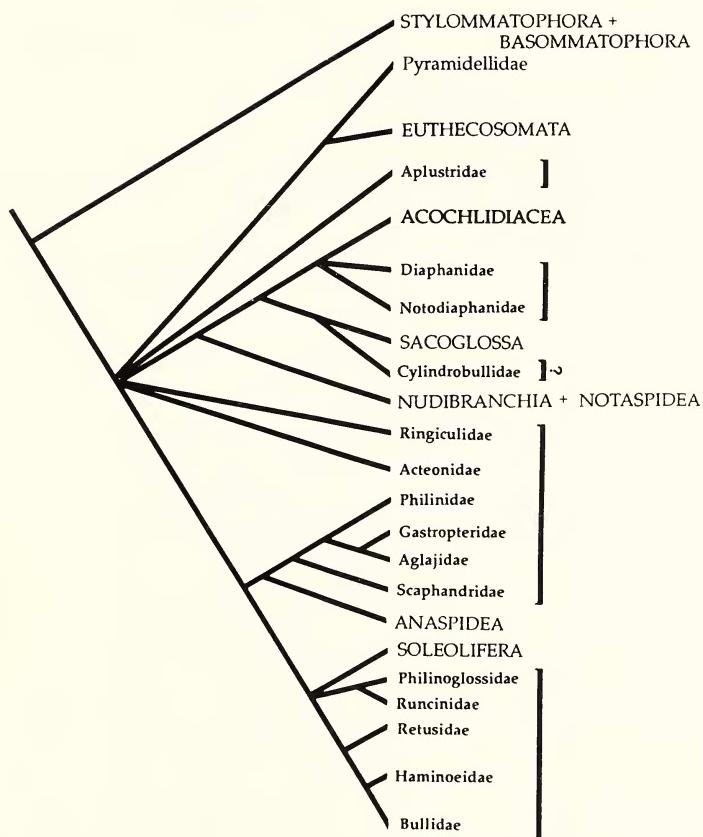


Figure 3. SALVINI-PLAWEN's (1970: fig. 1) phylogeny of euthyneuran gastropods [modified from Boettger (1955: fig. 1)], redrawn as a modern cladogram. Solid horizontal bar denotes present Cephalaspidea.

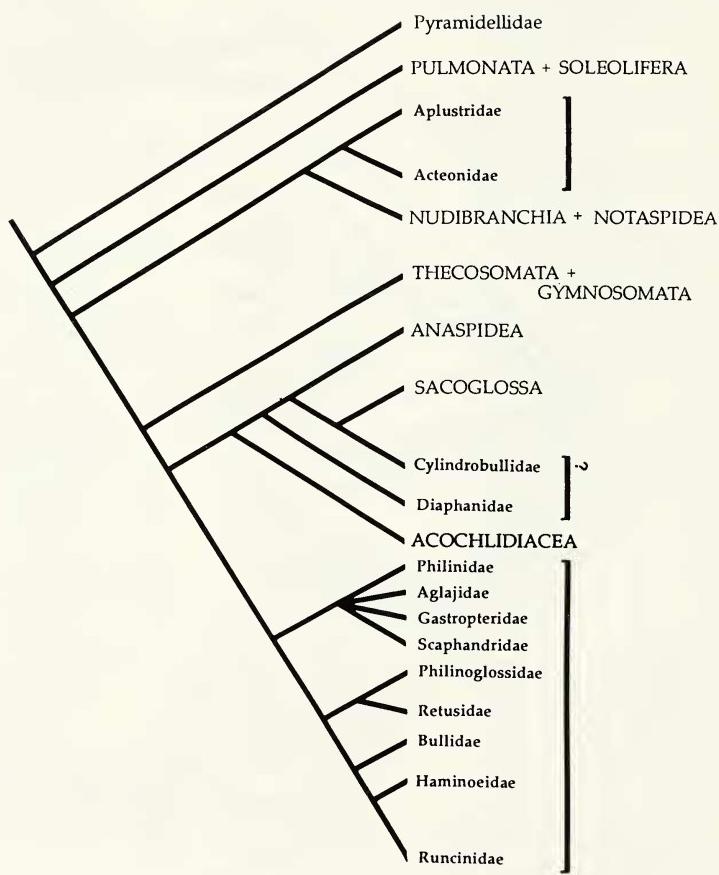


Figure 4. GHISELIN's (1966: fig. 7) «phylogenetic tree» of the Opisthobranchia, (based on a «functional analysis» of characters of the reproductive and alimentary systems), redrawn as a modern cladogram. Solid horizontal bar denotes present Cephalaspidea. Ringiculidae was not included on the original tree due to uncertain affinities.

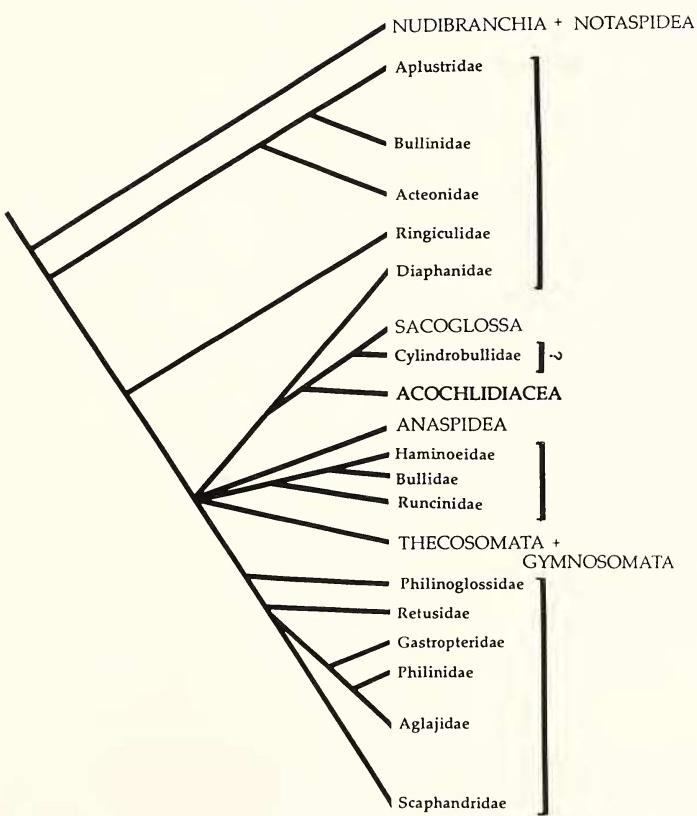


Figure 5. GOSLINER's (1978: pl. 22, fig. 36) phylogeny of the Opisthobranchia, redrawn as a modern cladogram. Solid horizontal bar denotes present Cephalaspidea.

	HP	R	C	F	I	HM
SHELL present/absent	B	x				
SHELL external/internal	B					
SHELL thick/thin	B	x				
SHELL not reduced/reduced	B	x				
SHELL exposed spire/involute/plate-like	B	x				
OPERCULUM present/absent	B	x				
CHROMOSOME number 12/17					x	
RETRACTION complete/incomplete	B		x			
CEPHALIC PROCESSES (form)	B			x		
MANTLE CAVITY position	B					
PALLIAL CAECUM short/long/absent	B					
PARAPODIA absent/weak/strong	B	x				
FOOT long/short	x	x				
POSTERIOR PALLIAL LOBE absent/present						
GILL present/reduced/absent	S	x				
GILL nonplicate/plicate						
HANCOCK'S ORGAN weakly/strongly developed						
HANCOCK'S ORGAN (form)			x			
LIP ORGANS (form)			x			
OSPHRADIUM not reduced/reduced	x?	x				
OSPHRADIUM (form)			x			
RADULA present/absent	D	x				
RADULA (form)	D			x		
RADULA teeth many/few	D	x				
RACHIDIAN present/absent	D	x				
JAWS present/absent	D	x				
JAWS armed/unarmed	D	x				
GIZZARD weakly/strongly developed	D					
GIZZARD PLATES absent/present	D					
GIZZARD PLATES 3/4/many	D					
GIZZARD PLATES (form)	D		x			
SALIVARY GLANDS 1/2 pair	D?					
ESOPHAGEAL DIVERTICULUM absent/present	D					
DIET carnivorous/herbivorous	D		x			
REPRODUCTIVE SYSTEM monaulic/diaulic	x		x			
COPULATORY ORGAN nonretractile/retractile	B					
PROSTATE pallial/genital	x					
SPERM DUCT open/closed	x?				x	
EJACULATORIAL DUCT open/closed	x					
SPERMATIC BULB absent/present	x					
RECEPTACULUM SEMINIS present/absent	x	x				
PALLIAL GONODUCT simple/divided						
GONODUCT pallial/coelomic						
NERVOUS SYSTEM streptoneurous/euthyneurous	S	x				
EYES present/absent	B	x				
NERVE RING pre-pharyngeal/post-pharyngeal	x					
NERVE RING ganglia 6/4	S	x				
VISCERAL LOOP long/short	S	x				
VISCERAL LOOP ganglia 5/4/3	S	x				

Table 2. Traditional cephalaspid characters used by 35 key classifications and proposed phylogenies, with the problems associated with their use in cladistic analysis. x = problem noted; C = condition; F = form; HM = homology; HP = presumed homoplasy (with suspected agent: B = burrowing; D = diet; S = small size); I = incomplete; R = reduction.

Traditional cephalaspid characters

Evaluation of the above-mentioned previous descriptions and phylogenograms yielded 49 frequently-utilized characters (Table 2).

Most the characters have been associated by various authors with the theoretically-homoplastic agents of burrowing (plus shell loss), diet, or small size (Table 2). Their derived states have been claimed to have «evolved» more than once during cephalaspid evolution (BOETTGER, 1955; GHISELIN, 1966; GOSLINER, 1978; GOSLINER & GHISELIN, 1984), giving rise to statements of «rampant parallelism» in the group (GOSLINER & GHISELIN, 1984). Much of this «evolution» is perceived as loss; twenty characters (42%) involve presumed reduction or loss of a feature. It must be argued here that, technically, one cannot invoke homoplasy to explain character distributions before the fact. Homoplasy is a phenomenon recognized through the analytical process, not an intrinsic quality of a character state. Because a rigorous phylogenetic analysis is not yet available for opisthobranchs, all cases of inferred homoplasy are products of *a priori* decisions at this point. One can certainly allow that the potential for homoplasy may be particularly high in certain cases, such as the absence of features, and take appropriate precaution. Absence or weak development of a character could also conceivably represent two different states: primary condition/absence or secondary loss/reduction.

Six characters reflect the general form or shape of a structure. This type of phenetic similarity requires better definition of the homologous characters and character states involved. Three broad functional or physiological «conditions» (carnivorous/herbivorous, monaulic/diaulic, retraction complete/incomplete) are similarly unusable. Each of these suggests probable suites of characters and questions of homology.

«Sperm duct open/closed» has a more obvious homology problem. Based on a reproductively monaulic «mesogastropod» ancestor, GHISELIN (1966: 333) stated that «the open seminal groove has been converted into a closed tube... called the vas deferens». This is a functional interpretation, reflecting analogy rather than homology. Based on positional evidence, the open external sperm groove, from the common genital opening to the copulatory organ opening, is probably not homologous with the closed pallial sperm duct (= «vas deferens»), extending from the common pallial gonoduct, through the prostate gland to the base of the copulatory organ. Both states apparently occur simultaneously in the sacoglossan *Ascobulla ulla* (MARCUS) (MARCUS, 1972). Therefore the connection/separation of the pallial sperm duct (with its associated prostate gland) from the common pallial gonoduct is distinct from the loss/gain of the external seminal groove.

Data on chromosome number are still too incomplete to be successfully used in this dataset, although considerable progress has been made since GHISELIN (1966) first considered its use (PATTERSON, 1969; NATARAJAN, 1970; VITTURI et al., 1985; CURINI-GALLETTI, 1985, 1988). Members of the cephalaspid genera *Bulla*, *Haminoea*, *Scaphander*, *Philine*, *Smaragdinella*, *Runcina*, and *Aglaja* have a haploid number of 17 or 18. This range is also generally found in Sacoglossa, Anaspidea, and basommatophoran and soleoliferan Pulmonata. However, Nudibranchia, the most thoroughly exa-

mined group so far (VITTURI *et al.*, 1985) shows a very consistent 13. Members of Notaspidea also possess 12 or 13. The only «architectibranch» examined so far [*Hydatina velum* (Gmelin)] has 15 (NATARAJAN, 1970). [NATARAJAN's (1970) statement that other acteonoideans have 17 chromosomes is apparently based on a species of *Cylichnatys*, now placed in Haminoeidae (BURN, 1978)]. *Philinoglossa praelongata* SALVINI-PLAWEN has 13 (CURINI-GALLETTI, 1985). Within the Heterostropha, Valvatidae reveal 10 and Pyramidellidae 17 (PATTERSON, 1969). In a recent review, VITTURI *et al.* (1985), suggested that chromosome number may be a highly stable character at family or higher taxonomic level in molluscs. But polarity is still in question: low number has been considered plesiomorphic (PATTERSON, 1969) or derived (CURINI-GALLETTI, 1985). This is definitely a character worth investigating further.

In summary, of the 49 traditionally most-used characters, 44 (90%) are here perceived as problematic. It is obvious then, that the dataset presented in Table 2 is insufficient for use in cladistic analysis, and it is therefore no surprise that authors emphasizing these characters have claimed that «it cannot be done».

Monophyletic subgroups?

Given the lack of recognized synapomorphies for Cephalaspidea, and the acknowledgment that only monophyletic taxa be formally recognized in classification, the entire order Cephalaspidea is now difficult to justify. However, in the phylogenograms generated using the above-discussed characters, are there any family groups which are consistent and/or defined by synapomorphies?

The polychotomies present in SALVINI-PLAWEN's (1970) and GOSLINER's (1978) trees severely limit the identification of possible monophyletic units. However, one consistent grouping is obvious: the superfamily Philinoidea (Philinidae + Scaphandridae + Gastropteridae + Aglajidae), which is also the most consistently recognized group in cephalaspid classifications. But synapomorphies for this group are difficult to discern from the three publications. SALVINI-PLAWEN (1970) and BOETTGER (1955), on which the former was based, identify nothing specific. GOSLINER (1978), who placed major importance on dietary morphology, found flattened gizzard plates to be unique when Retusidae was added to the group. When Philinoglossidae was also considered, a radula with enlarged cusp-like lateral teeth became synapomorphic for Philinoidea. Other superfamilial characteristics (carnivory, pre-pharyngeal nerve ring, monaulia, simple mucus gland) were symplesiomorphic according to GOSLINER. GHISELIN (1966) described only phenetic similarities in reproductive system structure and grades in reduction of the shell and radula, and suggested mosaic evolution patterns among the four families; but he also mentioned features at the cellular level (e.g., secretory cells of unknown function in coelomic gonoduct) which seem worthy of additional study. RUDMAN's (1978) discussion of phylogeny within the Philinoidea defined phenetic similarities and grades similar to those of GHISELIN.

The only other cephalaspid superfamily consistently used in classifica-

tions is also recognizable in all three trees: Bulloidea (Bullidae + Haminoeidae). SALVINI-PLAWEN (1970) added Retusidae and defined the group by possession of a shortened foot. GHISELIN (1966) added Runcinidae and used herbivory (with its associated esophageal diverticulum, which was however «lost» in Haminoeidae) as a synapomorphy. GOSLINER (1978) defined the same clade as GHISELIN, but added ridged gizzard plates and an elaborated mucus gland to the list of presumed synapomorphies.

In spite of these three attempts to redefine cephalaspids based on new data, most apparent synapomorphies for the few consistent groups are associated with diet, e.g., the «traditional» radulae and gizzard plates. Separate carnivorous and herbivorous lineages of cephalaspids were also advocated by GUIART (1901), PRUVOT-FOL (1954), GHISELIN (1966), RUDMAN (1971), KANDEL (1979), and SALVINI-PLAWEN (1988). HASZPRUNAR (1985) used herbivory and the resultant plate-bearing anterior gizzard as synapomorphies of his superorder Tectibranchia (=Cephalaspidea, plus others). And JENSEN (1991: 149) has acknowledged a number of alimentary characters as phylogenetically informative within the closely-related Sacoglossa (=Ascoglossa) in spite of «many specializations to specific diets». These observations support the belief of T.E. THOMPSON (1976) that dietary needs formed the driving force behind the successful radiation of opisthobranchs. However, several authors have cautioned against the use of alimentary characters at higher taxonomic levels. HASZPRUNAR (1985) implicated convergence through herbivory for the presence of a muscular stomach in two groups of non-tectibranch heterobranchs. BRACE (1977b: 51) noted «considerable anatomical similarity» in the alimentary systems of herbivorous cephalaspids and pulmonates. The «plasticity» of gastropod radulae in response to prey structure or habitat was summarized for prosobranchs by KOOL (1987). SALVINI-PLAWEN & HASZPRUNAR (1987) expressed the general opinion that characters of the gastropod digestive system are correlated more with diet than phylogeny (although useful characters were found in configuration of the esophagus). As previously mentioned, congruence of radular/gizzard plate morphology with diet has been noted in a preliminary survey of cephalaspids (MIKKELSEN, 1989, 1990). While diet-related morphology may reflect phylogenetic relationship in a well-defined specialist group as the Sacoglossa, the probability of homoplasy is undoubtedly higher for the much larger and ill-defined Cephalaspidea.

Possible New Taxonomic Characters

From the literature, several suggestions may be immediately put forth as potentially useful characters worthy of serious investigation: (1) karyotype (discussed above); (2) cellular morphologies within the reproductive tract (GHISELIN, 1966), e.g.: (a) ciliated strips in the ampullae of Acteonidae and nudibranchs which serve to bypass eggs around stored autosperm, and (b) secretory cells of unknown function noted in the coelomic gonoduct of philinoideans; (3) sperm ultrastructure and spermiogenesis, studied in only a few cephalaspids (THOMPSON, 1973; HEALY, 1982b), but proven informative in other heterobranch groups (HEALY, 1982a, 1988a,b; HEALY & WILLAN, 1991); (4) structure of spermatophores,

reported in *Haminoea* and *Runcina* (GHISELIN, 1966); (5) fine structure of osphradia (HASZPRUNAR, 1986, 1988, and pers.comm.) and Hancock's organ; (6) stomach structure; (7) muscular arrangements of the gizzard or buccal mass (GOSLINER & GHISELIN, 1984); and (8) details of the nerve ring complex (HUBER, 1987). Some of these data are already accessible or under study, but so far, no synthesis is available.

The complete resolution of problematic cases such as this may ultimately require the use of physiological, biochemical, and/or molecular data. At this taxonomic level, the most appropriate molecular method is currently gene sequencing, with the DNA molecule generally the preferred source (HILLIS, 1987; HILLIS & MORITZ, 1990: table 1). Unfortunately at the present time, these sophisticated techniques are fraught with technical difficulties in mucus-laden mollusks and have not been routinely applied to phylogenetic studies. Attesting to this, the first molecular (RNA-based) phylogenies involving gastropods have only recently been published (EMBERTON, *et al.*, 1990; TILLIER, *et al.*, 1992; summarized by BIELER, 1992). Even when molecular and other novel characters can be practically employed, these do not supersede morphological characters. Biochemical and molecular data are not immune from the effects of homoplasy (GHISELIN, 1988; MURPHY, 1988; SWOFFORD & OLSEN, 1990), and a sound morphology-based phylogeny must be available upon which to intelligently interpret results derived from other sources. Morphology is also critical to the moluscan systematist for the inclusion of imperfectly-known, rare and fossil taxa in the dataset. An integrated approach utilizing as many types of data as possible should ultimately provide the best resolution.

Conclusions

The chronic confusion in cephalaspisid systematics is a direct reflection of the persistent use of traditional characters, which are implicated in a variety of problems and have been thus far unable to demonstrate relationships. Successful resolution of the phylogeny of these and other «lower heterobranchs» will require (1) critical reevaluation of morphology to determine an improved set of taxonomically informative, homologous characters (irregardless of previous claims of homoplasy), and (2) looking beyond morphology to explore the use of innovative, non-traditional characters. Only thorough a through cladistic analysis can suspected parallelisms be confirmed and morphyletic clades identified.

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